PARTHENOGENESIS IN THE MAYFLY *STENONEMA FERMORATUM* (SAY)[1] EPHEMEROPTERA: HEPTAGENIIDAE)

W. P. McCafferty
and B. L. Huff, Jr.[2]

The first case of parthenogenesis in mayflies was demonstrated by Clemens (1922) for *Ameletus ludens* Needham from eastern North America. Clemens was able to observe larvae hatching from eggs taken from unmated female imagos thus confirming the existence of viable parthenogenetic offspring. Previous to this, Morgan (1911) had suggested that the above species was parthenogenetic based on the fact that male imagos were consistently missing from field collections. Only two male imagos of *A. ludens* are known to date and were reported by Needham (1924).

Britt (1962) showed experimentally that *Ephoron album* (Say) was partially parthenogenetic by obtaining 8 to 10 per cent hatch of eggs taken from virgin females reared in isolation. Numbers of male and female subimagos of this population taken in emergent tent traps by Britt in the field, however, were approximately equal indicating a sex ratio very unlike that of *A. ludens.*

Other North American mayflies which have been implicated with the phenomenon of parthenogenesis on the basis of observed sex ratios (predominately or entirely made up of females), but for which there is no direct experimental proof, include *Ephemerella rotunda* Morgan (Needham et al., 1935), *Ephemerella* sp. from Colorado (Dodds, 1923), and *Ameletus lineatus* Traver (Burks, 1953).

Sequential parthenogenetic generations have not been studied in *A. ludens* and *E. album* nor have cytogenetic analyses been undertaken. The distinct lack of males would indicate that the parthenogensis is possibly geographic, thelytokous, and obligatory in certain populations of *A. ludens;* whereas, the preponderance

---

[1]Published with the approval of the Director of the Purdue University Agricultural Experiment Station as Journal Series No. 5188. Accepted for publication: July 18, 1973.

[2]Department of Entomology, Purdue University, West Lafayette, Indiana 47907.

of sexual reproduction in *E. album* (Edmunds et al., 1956; and Britt, 1962) would signify a facultative situation.

The most complete study of parthenogenesis in Ephemeroptera species was carried out by Degrange (1960), wherein he demonstrated the existence of parthenogenesis in 26 of 51 species of European mayflies tested. The type of parthenogenesis was determinable for only three of the species examined (those amenable to being reared for at least two successive parthenogenetic generations in the laboratory). *Centroptilum luteolum* (Müller) was shown to be deuterotokous, while *Cloeon simile* Eaton and one other unidentified species of *Cloeon* were shown to be thelytokous. Degrange's work indicates that parthenogenesis is much more common and of more complex types in mayflies than had been previously thought. The genetic mechanisms involved and the influence of parthenogenesis on the reproductive potential of these species in nature have not been shown.

Certain preliminary observations in the summer of 1971, in conjunction with a study of the biology and ecology of local species belonging to the genus *Stenonema*, prompted consideration of parthenogenesis as a possibly alternate means of natural reproduction in this genus. Constant field inspection had not yielded any observable instances of either swarming or mating in local *Stenonema* populations, yet female imagos were regularly seen ovipositing on the stream surface. We have recently — May, 1973 — witnessed swarming; and mating flights in *Stenonema* have occasionally been reported, e.g. Cooke (1940) and Thew (1958). Any conclusions drawn from our earlier observations alone can be criticized since they may have been coincidental to nonactive periods. However, when such observations were taken into consideration with the following laboratory events they became more convincing inferential evidence.

Female imagos reared from field collected larvae would attempt to oviposit eggs after a period of time and without any prior opportunity for fertilization by a male. Abdominal fibrillation in captive unmated females would proceed on a dry lab bench and partial evacuation of eggs would occur if the females were then placed on a water surface. It could be surmised from this observation that oviposition, irrespective of whether or not the eggs had been fertilized, would proceed either as a response to some stimulus not related to copulation or simply as an innate

behavioral mechanism. Oviposition with no chance of egg hatch would seem to be a rather useless and energy consuming evolutionary strategy in a population. A reasonable alternative explanation, therefore, was that there might indeed be present the potential for parthenogenetic reproduction which would insure continuation of the lineage and have adaptive significance. Degrange (1960) found that in several species, virgin females with parthenonenetic eggs would not oviposit in captivity. The lack of oviposition behavior in virgin females cannot therefore be correlated with the presence or absence of parthenogenesis; however, the presence of such behavior in virgins may be a strong evidence for parthenogenesis.

The paucity of information on conditions necessary for normal eclosion of fertilized eggs of *Stenonema* made any experimental design to test for eclosion of unfertilized eggs suspected of being parthenogenetic somewhat haphazard. Our first attempts to gain hatchings from eggs extracted from virgin females of *Stenonema* were made in the summer of 1971. Eggs from *S. femoratum* (Say), *S. nepotellum* (McDunnough), and *S. vicarium* (Walker) were incubated at room temperature for 60 days with no hatchings observed. Recently, however, under more controlled conditions we were able to confirm parthenogenesis in one species.

A series of larvae of *S. femoratum* were collected as follows: Indiana: Jefferson Co., Clifty Creek at Rt. 56, III - 6 - 1973, A.V. Provonsha, collector. The larvae were placed in aerated rearing aquaria and maintained at a temperature of between 72 and 74 F. A solitary female subimago emerged and was immediately isolated in a separate subimago rearing chamber. This individual moulted to the imago approximately 24 hours later. Following another period of 36 hours from the time of the imaginal moult, the individual female was placed on the surface of water in a Petri dish and voluntarily discharged a few eggs. Subsequent dissection yielded most of the remaining eggs. The eggs were then placed in stream water taken at the site of the larval habitat. All incubating eggs were checked under a microscope periodically thereafter. Live larvae were discovered 24 days after incubation was begun. We were unable to keep the newly hatched larvae alive for any extended period of time, and could not determine sex. A tabular summary of conditions and results follows:

Stenonema femoratum (Say)

Emergence of female subimago		III-23-1973
Imaginal moult		III-24-1973
Oviposition by female		III-25-1973
Number of eggs incubated		487
Incubation temperature		68-70 F
Light/dark incubation cycle		14 hrs./10 hrs.
Larval hatch:	4	IV-18-1973
	1	IV-20-1973
	1	IV-23-1973
Post-oviposition embryonic development		24-29 days
Total larval hatch		6
Per cent hatch		1.23

This represents the first reported incidence of parthenogenesis for the genus *Stenonema*, and the third such demonstrated case for North American mayfly species. Degrange (1960) was able to show the existence of parthenogenesis in nine species of the heptageniid genera *Epeorus*, *Ecdyonurus*, *Rhithrogena*, and *Heptagenia*. The per cent of parthenogenetic hatch in these species ranged between 0.18 and 4.46, and in most cases was less than 1.0 per cent hatch. The preliminary data we have for *Stenonema* fits within the above range, and this percentage could conceivably be significant in terms of the population dynamics of this species.

Because the parthenogones of *S. femoratum* died before they were mature enough to be sexed, the type of parthenogenesis is not known. Nevertheless, since sexual reproduction is also found in *S. femoratum* and our preliminary estimate of male to female sex ratio is 1:1, the parthenogenesis may be considered facultative and deuterotokous. Until such time that parthenogones can be shown to live to maturity there remains the remote possibility that the parthenogenesis is of the rudimentary type. Dr. George F. Edmunds, Jr., University of Utah, (Personal communication, 14 May 1973) has pointed out to us that the low percentage of parthenogenetic hatch in so many of the species studied may correspond to the small proportion of those naturally occurring diploid eggs which have not undergone meiosis, and if normally fertilized potentially give rise to triploid individuals. There is only very indirect evidence for this at the present, however.

The results presented herein must be considered preliminary and possibly of limited application except for the mere demonstration of the presence of the phenomenon under consideration. Further study into the reproductive biology of *Stenonema* and the role of parthenogenesis is actively underway. The study of the

effect if any of parthenogenesis on the phenotypic character distribution in this taxonomically difficult and ecologically important group is worthy of continued effort and may help to explain historically inadequate species interpretations. Furthermore, the study of behavioral mechanisms as they relate to parthenogenesis in *Stenonema* might well prove rewarding, since Tjonneland (1970) has presented preliminary evidence indicating the decay of diel emergence, flight, and oviposition patterns in certain parthenogenetic aquatic insects.

LITERATURE CITED

BRITT, N. W. 1962. Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. Bull. Ohio Biol. Surv. 1: iv, 1-70.

BURKS, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bull. Ill. Nat. Hist. Surv. 26: 1-216.

CLEMENS, W. A. 1922. A parthenogenetic mayfly *(Ameletus ludens* Needham). Canad. Entomol. 54: 77-78.

COOKE, J. G. 1940. Observations on mating flights of the mayfly *Stenonema vicarium* (Ephemerida). Entomol. News. 51: 12-14.

DEGRANGE, C. 1960. Recherches sur la reproduction des Ephéméroptères. Trav. Lab. Hydrobiol. Grenoble 51: 7-193.

DODDS, G. S. 1923. Mayflies from Colorado. Trans. Amer. Entomol. Soc. 49: 93-114.

EDMUNDS, G. F., JR., L. T. NIELSEN and J. R. LARSEN. 1956. The life history of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae). Wasmann J. Biol. 14: 145-153.

MORGAN, A. H. 1911. Mayflies of Fall Creek. Ann. Entomol. Soc. Amer. 4: 93-126.

NEEDHAM, J. G. 1924. The male of the parthenogenetic mayfly *Ameletus ludens.* Psyche. 31: 308-310.

NEEDHAM, J. G., J. R. TRAVER and YIN-CHI-HSU. 1935. The biology of mayflies. Comstock Publ. Co., Ithaca. xvi + 759 pp.

THEW, T. B. 1958. The mating flights of *Ephoron album* (Say) and *Stenonema canadense* (Walker). Fla. Entomol. 41: 9-12.

TJONNELAND, A. 1970. A possible effect of obligatory parthenogenesis on the flight activity of some tropical larvo-acquatic insects. Årbok Univ. Bergen, Mat. - Naturvit. Ser. 1970(3): 3-7.

ABSTRACT – Parthenogenesis has been confirmed for the heptageniid mayfly, *Stenonema femoratum* (Say) by obtaining larval hatches from eggs taken from a reared unmated female imago. This represents the third demonstrated case of parthenogenesis in North American mayflies and the first such case for the genus *Stenonema.* Preliminary results are comparable to those obtained for European species of Heptageniidae in which parthenogenesis has been studied. Discussion of known cases of mayfly parthenogenesis and associated biology is included. McCafferty, W. P. and B. L. Huff, Jr., Department of Entomology, Purdue University, West Lafayette, Indian 47907.

Descriptors: Parthenogenesis, Stenonema, Heptageniidae, mayflies, reproductive biology.